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BIONOMICS AND BEHAVIOR OF *ALLOXYSTA MEGOURAE*, AN APHID HYPERPARASITOID (HYMENOPTERA: ALLOXYSTIDAE)

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Abstract.—The authors studied *Alloxysta megourae* (Ashmead), a hyperparasitoid of the pea aphid, *Acyrthosiphon pisum* (Harris). Larval, prepupal, and pupal stages of the primary parasitoid (*Aphidius smithi*) found in non-mummified aphids are attacked by *A. megourae*. Several aspects of *A. megourae* development within its host differ from those described in other species of *Alloxysta*. The sensory structures on the tip of the ovipositor of *A. megourae* are described.

Introduction

Several hymenopteran families are aphid hyperparasitoids. These aphid hyperparasitoids can be divided into two categories based on their attack behavior. (1) *Endoparasitoids*: the female oviposits in the primary parasitoid larva and then the hyperparasitoid larva feeds internally. (2) *Ectoparasitoids*: the female oviposits on the surface of the primary parasitoid and then the hyperparasitoid larva feeds externally. We studied *Alloxysta megourae* (Ashmead), an endoparasitoid of *Aphidius smithi*.

The classification of *Alloxysta* was studied by Andrews (1978). Haviland (1921) was the first to comment on the relationship among three species of Alloxystidae (given as Cynipidae) and their primary parasitoid host. The embryology and larval development of *Alloxysta* (given as *Charips*) was described by Haviland (1921). Gutierrez and van den Bosch (1970a, b), Gutierrez (1970a–d), Sullivan and van den Bosch (1971) and Sullivan (1972) studied *Alloxysta* (*Charips*) *victrix* in the field and laboratory. The bionomics and behavior of *Alloxysta megourae* have not been reported before. The sensory apparatus on the ovipositor of *A. megourae* is described.

Materials and Methods

The pea aphid, *Acyrthosiphon pisum* (Harris), served as the host in this study, and was reared on broad bean, *Vicia fava* L. (Windsor variety).

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Table 1. Composite life cycles of the primary parasitoid, *Aphidius smithi*, and the hyperparasitoid, *Alloxysta megourae*, under laboratory conditions.

Age in days	*Aphidius smithi*	Age in days	*Alloxysta megourae*
0	Egg deposited in aphid		
1			
2	1st larval instar		
3			
4	2nd larval instar		
5			
6	3rd larval instar	0	Egg deposited in *Aphidius*
7		1	
8	Host aphid mummified[a]	2	Egg hatches (host aphid mummified)
9		3	
10	Prepupa (meconium voided)	4	1st larval instar
11	Pupa	5	
12	Adult emerges	6	2nd larval instar
		7	
		8	3rd larval instar
		9	
		10	Mature larva feeds externally
		11	
		12	Prepupa (meconium voided)
		13	Pupa
		14	
		15	
		16	
		17	
		18	
		19	Adult emerges

[a] When hyperparasitized by *Alloxysta*, *Aphidius* ceases development.

Aphidius smithi Sharma & Subba Rao, the primary parasitoid, and *Alloxysta megourae* (Ashmead), the hyperparasitoid, were reared with the plants and aphids in a bioclimatic chamber (Percival Environator, Model E-54U) according to the method described by Bennett and Sullivan (1978).

The daytime (16 hr) temperature was 21.1 ± 0.6°C at 75 ± 5% RH. At night the temperature was 15.5 ± 0.6°C at 85 ± 5% RH.

The primary parasitoid, *Aphidius smithi*, was reared by placing 2–4 mated females in a glass tube with cut broad bean stems and 20 4th instar pea aphids. The tube was kept in the bioclimatic chamber for 6 hr. Then the wasps were removed and the parasitized aphids replaced on the broad bean leaves and returned to the temperature chamber. After 12 days, the adult *Aphidius* emerged from the aphids.

To observe the process of courtship and mating, the adult *Alloxysta* male and female were left undisturbed for 6 hr in the Dixie container. We ob-

served oviposition by placing 5–6 adult *Alloxysta* females in a 60 × 15 mm plastic Petri dish with 15 4th instar aphids. The life cycle of *A. megourae* (Table 1) was studied by a technique allowing continuous observation of all stages of development within the aphid mummy (Keller & Sullivan, 1976).

To determine whether *A. megourae* females attack both parasitized and unparasitized aphids, we placed a female *Alloxysta* in a Petri dish for 3 hr with a parasitized aphid having a 6–7-day-old *Aphidius* larva and an unparasitized aphid. All aphids used in 50 replicates were in the 4th instar. After the *Alloxysta* was removed, we dissected and recorded the eggs in each aphid.

Results and Discussion

Courtship and Mating

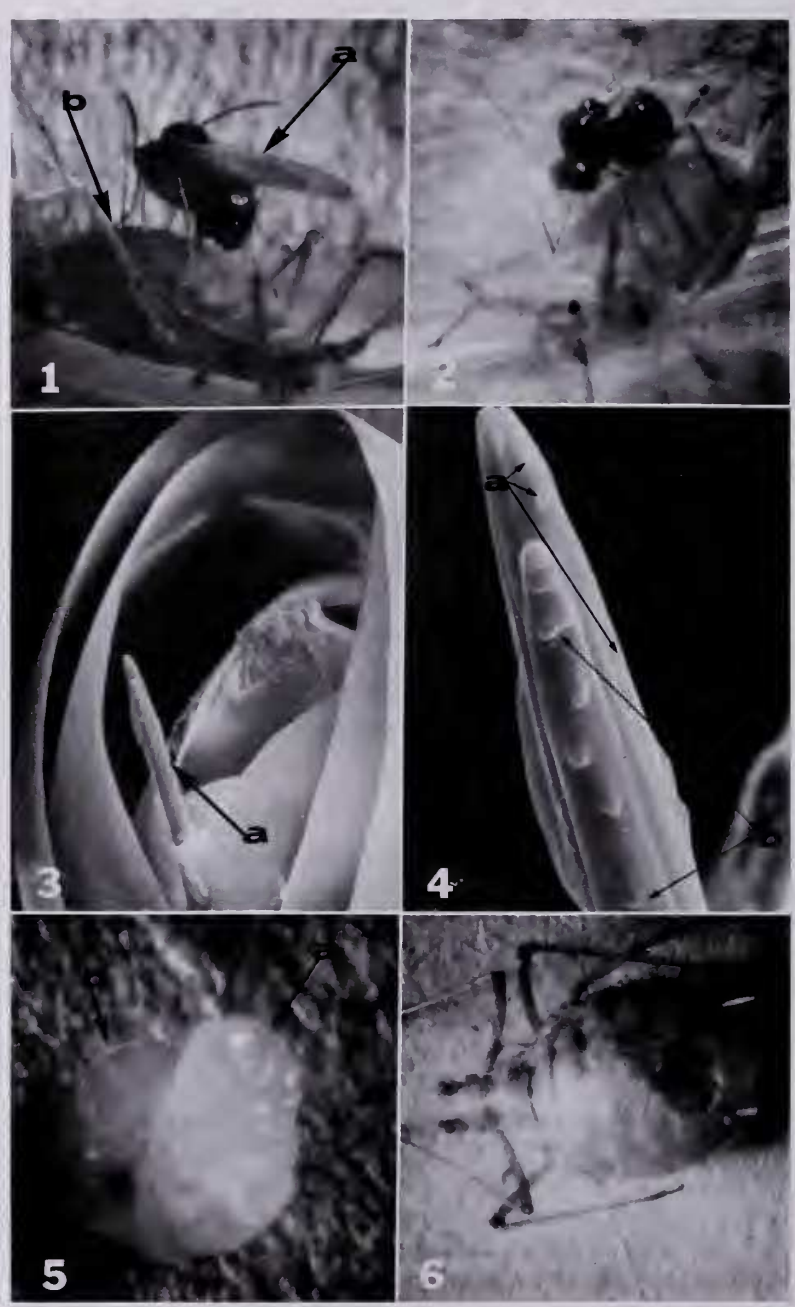
Alloxysta adults were able to mate soon after emergence. The courtship begins when the male follows the female around the observation chamber. His behavior was predictable: he positioned himself behind the female and tapped her abdomen with his antennae, while she remained motionless. This phase lasted from 2–7 minutes. More intensified courtship began when the male mounted the female. He climbed on her back with his legs firmly grasping the sides of her body. Pairs were frequently observed mounted, with the male on top of the female and being carried about by the female for as long 30 seconds to 1 minute. Copulation lasted from 10–20 seconds.

Oviposition Behavior

A. megourae behaves as an endoparasitoid. It attacks the *Aphidius* larva, which has been developing inside a live aphid, and deposits the egg within the primary parasitoid larva.

The egg-laying behavior of *A. megourae* has the following pattern: the female approaches the live parasitized aphid and rapidly antennates its surface. She then mounts the back of the aphid and assumes a squatting position with her abdomen slightly bent (Fig. 1). Once the *Alloxysta* female secures herself tightly on the dorsum of the aphid, the aphid moves violently as if trying to dislodge the wasp. She then inserts her ovipositor through the thin exoskeleton of the aphid and probes the aphid's hemocoel in search of the primary parasitoid larva (Fig. 2). If unsuccessful at that site, the *Alloxysta* female withdraws the ovipositor, moves to a new position on the aphid's dorsum and begins to probe again for the host. *A. megourae* females have not been seen to host-feed, neither before nor after oviposition nor do they paralyze their hosts.

It was not unusual to observe 4–5 *Alloxysta* females ovipositing at the same time on the same live, parasitized aphid. They were not easily dis-


a
b
1
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6

urbed when ovipositing, even when some *Alloxysta* females climbed over ınd under each other while others were ovipositing. Once situated on the ıphid, all 4 or 5 *Alloxysta* females probe simultaneously for the primary ɔarasitoid within the aphid. Invariably, although several eggs may be laid, ɔnly one adult developed from each host. Once oviposition is completed, he *Alloxysta* female withdraws her ovipositor and abruptly leaves the ıphid.

Sensory Structures on Ovipositor

Scanning electron micrographs of the sensory structures on the ovipositor ɔf *A. megourae* are seen in Figs. 3 and 4. The ovipositor is composed of ɔaired 1st valvulae, and a fused pair of ventral 2nd valvulae. Each of the st valvulae has three sensory pits. The 2nd valvulae have barbs on the ɔuter surface, but no pits.

Development within the Mummy

Eclosion of the *Alloxysta* larva from the egg occurs about 72 hr after nummy formation and is encased within a white, opaque mass. The larva s translucent white with visible segmentation on the surface. It undergoes everal instars, and as the larva increases in size, a color change is evident. t becomes bright yellow, almost indistinguishable from the yellow *Aphidius* arva.

By the 9th day after *Alloxysta* egg deposition, the surface of the *Aphidius* arva begins to change to a dark brown color, it appears wrinkled and slowly leteriorates. On the 10th day, the *Alloxysta* larva emerges from the *Aphi- ius* larva and begins to feed externally on it (Fig. 5). By the end of the 11th lay, the entire *Aphidius* larva is consumed with the exception of the head apsule which is pushed to one side of the mummy. On the 12th day, the nidgut and hindgut of *Alloxysta* are connected and the meconium is voided nd is pushed against one side of the mummy. This begins the prepupal

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Figs. 1–6. Ovipositional behavior and developmental stages of *Alloxysta megourae*. 1. Adult *Alloxysta* female exhibiting a typical drilling position (a) on the parasitized pea aphid b). The head is down and the legs are firmly attached on the aphid's dorsum. (25×) 2. Adult emale *Alloxysta* ovipositing with antennae extended straight back. (25×) 3. Scanning electron nicrograph of the abdomen of an *Alloxysta* female with the ovipositor evident (a). (200×) 4. Scanning electron micrograph showing details of the structures located on the tip of an *Alloxy- ta* ovipositor. Three sensory pits (a) on the 1st valvulae and a row of barbs (b) on the fused 2nd valvulae are shown. (1000×) 5. A 10-day-old *Alloxysta* larva (a) emerging from its host, *Aphidius* (b), which it consumes within a few hours. (80×) 6. The characteristically irregular exit hole of *Alloxysta* located on the posteriodorsal side of the aphid mummy. (50×)

Table 2. Discrimination between parasitized and unparasitized aphids by the hyperparasitoid female *Alloxysta megourae* for oviposition (based on 50 replicates).

	Time in min. probing	Std. Dev.	No. of reinsertions	Std. Dev.	No. eggs laid	Std. Dev.
Parasitized	8.0	2.80	4.0	0.21	2.7	0.23
Unparasitized	5.6	2.71	3.4	0.25	0	0

stage which lasts about 24 hr. On the 13th day, the pupa is formed. It is bright yellow, but within 4–5 days, it gradually becomes dark brown. During this pupal stage, the hyperparasitoid was completely motionless. However, it did exhibit abrupt jerking movements if touched with a probe.

The adult *Alloxysta* emerges from the aphid mummy about 19 days after oviposition. The irregular-shaped emergence hole made by the *Alloxysta* adult was almost always located on the dorsal side of the aphid mummy (Fig. 6). Once emerged, the *Alloxysta* adult cleaned itself, fed on the honey-water mixture, and then began the courtship and mating behavior.

Discrimination between Parasitized and Unparasitized Aphids

The parasitoid attack behavior of *Charips* (*Alloxysta*) (Haviland 1921, Gutierrez and van den Bosch 1970b) is similar to that of *A. megourae*. However, Haviland (1921) reported that *Charips* selected only aphids containing a primary parasitoid whereas unparasitized aphids were ignored. Gutierrez (1970a) reported that *Charips victrix* (Westwood) probed unparasitized aphids. We found that *A. megourae* females always attacked and probed live aphids, both parasitized and unparasitized. These aphids were then dissected and in the 50 replicates, an average of 2.7 eggs were found in the *Aphidius* larvae, while no eggs were found in the unparasitized aphids (Table 2). Hence, discrimination appears to be accomplished during probing of the aphid with the ovipositor.

These data indicate several points: (1) *Alloxysta* females attacked unparasitized aphids but did not oviposit. (2) *Alloxysta* females attacked parasitized live aphids containing the *Aphidius* larva and would readily oviposit within the primary parasitoid host. However, the host larva may not always be detected since it may be in an inaccessible part of the aphid's hemocoel. In these situations, *A. megourae* changes position on the aphid's dorsum and probes and searches the hemocoel again (Gutierrez 1970a). Thus, not only does *Alloxysta* attack the same parasitized aphid more than once (Sullivan 1972) but a variable number of eggs are laid in the *Aphidius* larva within the aphid as a result of these attacks. A study of Table 2 would seem to indicate that there is no direct correlation between the number of ovipositional attempts and the actual number of eggs deposited.

Sensory Structures on Ovipositor

It has been known that sensory structures are important in host selection and host discrimination. Muesebeck and Dohanian (1927) stated that hyperparasitoids are less discriminatory than primary parasitoids in host selection. But, Gutierrez (1970d) showed that the ovipositor of *A. victrix* has sensory structures near the tip which apparently are used by this hyperparasitoid to discriminate among different species of primary parasitoid host larvae. In our study, *A. megourae* showed a similar morphology of the ovipositor. The 3 sensory pits are sensilla coeloconica as described by Snodgrass (1935) and Chapman (1969). However, in addition to Gutierrez' mention of the sensory pits on the paired 1st valvulae which probably have a chemosensory function, our photomicrographs also show 8 or more barbs on the outer surface of the 2nd valvulae. Probably these barbs anchor the 2nd valvulae during oviposition, while the 1st valvulae are inserted into the aphid's hemocoel in order to search for the *Aphidius* larva.

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